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Two new genera and species of river snails from the upper Changjiang River Basin in China (Gastropoda, Viviparidae)

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Abstract

Two new genera, *Shupaludina* Z.-G. Chen, Y.-T. Dai, H. Chen & X.-P. Wu, **gen. nov.**, and *Bapaludina* Z.-G. Chen & Y.-S. Guo, **gen. nov.**, and two new species, *Shupaludina luzhouensis* Z.-G. Chen & Y.-S. Guo, **gen. et sp. nov.**, and *Bapaludina dazhouensis* Z.-G. Chen & Y.-S. Guo, **gen. et sp. nov.**, of river snails are described from the upper Changjiang River Basin in China based on comparative morphology and molecular phylogeny. The two new genera have similar shell morphology and can be distinguished from other genera of the subfamily by common features such as a small- to medium-sized shell, a blunt apex, inflated whorls, the inner lip of the aperture folded and tightly overlapping the columellar margin, completely covering the umbilicus and forming with growth a crescent-shaped fortification (even in juvenile specimens), and an operculum much smaller than the aperture. They can be distinguished from each other by the presence or absence of keels on the teleoconch, differences in the size of the crescent-shaped fortification, differences in the size of the operculum, and differences in the radula. The discovery increases the known diversity of river snails in the upper Changjiang River.

Key Words

Biodiversity, freshwater, molluscs, phylogeny, taxonomy

Introduction

River snails (Viviparidae Gray, 1847) encompass small to large species of freshwater gastropods with a nearly global distribution, except for Antarctica and South America (Stelbrink et al. 2020; Zhang 2024). China represents a diversity hotspot of the family, harboring 14 genera and about 50 species (Yen 1939, 1943; Liu et al. 1979; Zhang et al. 2015, 2023, 2025; Zhang 2024). The upper Changjiang River (Yangtze) Basin, located in southwestern China, is a region of high diversity, with a total of five genera recorded: *Rivularia* Heude, 1890 (unpublished data from Zhong-Guang Chen), *Cipangopaludina* Hannibal, 1912, *Margarya* Nevill, 1877, *Sinotaia* Haas, 1939, and *Dalipaludina* Zhang, 2023 (Yen 1939, 1943; Liu et al. 1979; Lu et al. 2014; Zhang et al. 2015, 2023, 2025; Zhang 2024). Of these genera, only *Rivularia* belongs to the subfamily Viviparinae Gray, 1847, while the remaining four belong to the subfamily Bellamyinae Rohrbach, 1937 (Van Bocxlaer et al. 2018; Stelbrink et al. 2020).

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For a long time, the large river snails inhabiting the upper Changjiang River Basin in Yunnan have been a focal point of research endeavors (Yen 1939, 1943; Liu et al. 1979; Du et al. 2013; Lu et al. 2014; Shen et al. 2015; Tian et al. 2015; Zhang et al. 2015, 2023), while the species present within the same basin in Sichuan have received comparatively limited attention (Zeng et al. 1985).

During surveys conducted from 2019 to 2025, we collected 135 specimens of river snails from five localities in Sichuan. Based on a combination of morphology and molecular phylogeny, we describe two new genera and species of the subfamily Bellamyinae. Our study increases knowledge of the diversity of river snails in the upper Changjiang River.

Materials and methods

Specimens were collected from Sichuan, China, from 2019 to 2025. Living specimens were initially frozen at −20 °C for 24 hours and subsequently thawed at room temperature for 12 hours to facilitate the extraction of soft parts. The soft parts were then fixed in 95% ethanol. Empty shells were cleaned, dried, and preserved at room temperature. The aperture is oblique, and aperture height (outer height) is defined as the distance between the most apical and abapical points, rather than the distance projected in the plane of the columellar axis (as visible in figures of shells in apertural view). The radula was digested with proteinase K at 56 °C for 2 hours, then washed in deionized water. Prior to scanning electron microscopy (SEM), the early teleoconch and radula were dried in a clean environment for 8 hours, after which their surfaces were coated with gold. The samples were then examined via SEM (Thermo Fisher Quattro C, US). Photographs were taken with a Sony A7CII camera and edited in Adobe Photoshop CC 2015 (Adobe, San Jose, US). Maps were created in ArcGIS Pro (Esri, Redlands, US).

Genomic DNA was extracted from foot tissues preserved in 95% ethanol using a Qiagen DNeasy Animal DNA Kit (Qiagen, Germany). The quality and concentration of DNA were checked on 1% agarose gel electrophoresis and a NanoDrop 2000 (Thermo Scientific, US). Partial cytochrome c oxidase subunit 1 (*COI*) was amplified and sequenced for molecular phylogenetic analyses. Polymerase chain reaction (PCR) systems, conditions, and primer pairs followed Zhang et al. (2023). The *COI* sequences were aligned using MEGA v. 6.0 (Tamura et al. 2013). All sequences used in this study and their NCBI GenBank accession numbers are provided in Table 1.

Phylogenies were reconstructed with the *COI* dataset using maximum likelihood (ML) and Bayesian inference (BI). *Viviparus contectus* (Millet, 1813) was used as the outgroup for rooting the trees. Gene partitions and the best-fit substitution models were calculated with PartitionFinder2 v. 1.1 (Lanfear et al. 2017), based on the corrected Akaike Information Criterion (AICc) and using a heuristic search algorithm. The program proposed the division of the concatenated dataset into two partitions, comprising the first and second codon positions of the *COI* gene and the third codon position of the *COI* gene. The best-fit model was determined to be GTR+I+G for the first and second codon positions, while GTR+G was selected for the third position. ML analyses were performed in IQ-TREE v. 1.6.12 (Minh et al. 2013) using the ultrafast bootstrap approach (Minh et al. 2013) with 10,000 iterations. BI analysis was conducted in MrBayes v. 3.2.6 (Ronquist et al. 2012). Four simultaneous runs with four independent Monte Carlo Markov Chains (MCMC) were implemented for 10 million generations, and trees were sampled every 10,000 generations with a burn-in of 25%. Convergence was checked with an average standard deviation of split frequencies < 0.01 and a potential scale reduction factor (PSRF) ~ 1. Trees were visualized in FigTree v.1.4.3 (http://tree.bio.ed.ac.uk/software/figtree/).

Abbreviations. NCUMB: Museum of Biology, Nanchang University (Nanchang, Jiangxi, China); ZMNH: Zhejiang Museum of Natural History (Hangzhou, Zhejiang, China); IHB: Museum of Aquatic Organisms, Institute of Hydrobiology, Chinese Academy of Sciences (Wuhan, Hubei, China); SAFS: Museum of Aquatic Organisms, Sichuan Academy of Forestry Sciences (Chengdu, Sichuan, China); ASIZB: Institute of Zoology, Chinese Academy of Sciences (Beijing, China); MCZ: Museum of Comparative Zoology, Harvard University (Cambridge, Massachusetts, US); SH: shell height; SW: shell width; AH: aperture height; AW: aperture width; OH: operculum height; OW: operculum width; CT: central teeth; LT: lateral teeth; IMT: inner marginal teeth; OMT: outer marginal teeth.

Results

Phylogenetic analyses

The sequence dataset, consisting of 54 *COI* sequences from 30 species and subspecies, including one outgroup taxon, was employed for phylogenetic analyses. The alignment of *COI* had a length of 597 characters. Within this alignment, 235 sites were variable and 196 sites were parsimony informative (Suppl. material 1). The Bayesian and maximum likelihood analyses produced largely similar phylogenies (Fig. 1). *Shupaludina* gen. nov. is the sister group of the genus *Dalipaludina* Zhang, 2023, with high support (BS/PP = 91/0.98), while *Bapaludina* gen. nov. is the sister group of the genus *Sinotaia* Haas, 1939, with moderate support (BS/PP = 83/0.71). The p-distances of *COI* sequences between the 17 genera of Bellamyinae range from 5% to 17.6% (Suppl. material 2). The p-distance of *COI* sequences between the two species of *Shupaludina* gen. nov. is 2.33%, which is close to the p-distances among species in the sister group *Dalipaludina* (1.81%–3.98%).

Table 1. GenBank accession numbers of sequences used in this study.

Species	Accession numbers	Locality	References
Shupaludina magnaciana gen. & comb. nov. ind 1	PV365331	Baimuhe River, Pidu, Chengdu, Sichuan, China	this study
Shupaludina magnaciana gen. & comb. nov. ind 2	PV365332	Baimuhe River, Pidu, Chengdu, Sichuan, China	this study
Shupaludina magnaciana gen. & comb. nov. ind 3	PV365333	Baimuhe River, Pidu, Chengdu, Sichuan, China	this study
Shupaludina magnaciana gen. & comb. nov. ind 4	PV365334	Baimuhe River, Pidu, Chengdu, Sichuan, China	this study
Shupaludina magnaciana gen. & comb. nov. ind 5	PV365335	Baimuhe River, Pidu, Chengdu, Sichuan, China	this study
Shupaludina magnaciana gen. & comb. nov. ind 6	PV365336	Baimuhe River, Pidu, Chengdu, Sichuan, China	this study
Shupaludina magnaciana gen. & comb. nov. ind 7	PV365337	Baimuhe River, Pidu, Chengdu, Sichuan, China	this study
Shupaludina magnaciana gen. & comb. nov. ind 8	PV365338	Baimuhe River, Pidu, Chengdu, Sichuan, China	this study
Shupaludina luzhouensis gen. & sp. nov. ind 1	PX111720	Huagaoxi River, Shuiwei, Luzhou, Sichuan, China	this study
Shupaludina luzhouensis gen. & sp. nov. ind 2	PX111721	Huagaoxi River, Shuiwei, Luzhou, Sichuan, China	this study
Shupaludina luzhouensis gen. & sp. nov. ind 3	PX111722	Huagaoxi River, Shuiwei, Luzhou, Sichuan, China	this study
Shupaludina luzhouensis gen. & sp. nov. ind 4	PX111723	Huagaoxi River, Shuiwei, Luzhou, Sichuan, China	this study
Shupaludina luzhouensis gen. & sp. nov. ind 5	PX111724	Huagaoxi River, Shuiwei, Luzhou, Sichuan, China	this study
Shupaludina luzhouensis gen. & sp. nov. ind 6	PX111725	Huagaoxi River, Shuiwei, Luzhou, Sichuan, China	this study
Shupaludina luzhouensis gen. & sp. nov. ind 7	PX111726	Huagaoxi River, Shuiwei, Luzhou, Sichuan, China	this study
Shupaludina luzhouensis gen. & sp. nov. ind 8	PX111727	Huagaoxi River, Shuiwei, Luzhou, Sichuan, China	this study
Bapaludina dazhouensis gen. & sp. nov. ind 1	PX111712	Tongbohe River, Tongchuan, Dazhou, Sichuan, China	this study
Bapaludina dazhouensis gen. & sp. nov. ind 2	PX111713	Tongbohe River, Tongchuan, Dazhou, Sichuan, China	this study
Bapaludina dazhouensis gen. & sp. nov. ind 3	PX111714	Tongbohe River, Tongchuan, Dazhou, Sichuan, China	this study
Bapaludina dazhouensis gen. & sp. nov. ind 4	PX111715	Tongbohe River, Tongchuan, Dazhou, Sichuan, China	this study
Bapaludina dazhouensis gen. & sp. nov. ind 5	PX111716	Tongbohe River, Tongchuan, Dazhou, Sichuan, China	this study
Bapaludina dazhouensis gen. & sp. nov. ind 6	PX111717	Tongbohe River, Tongchuan, Dazhou, Sichuan, China	this study
Bapaludina dazhouensis gen. & sp. nov. ind 7	PX111718	Tongbohe River, Tongchuan, Dazhou, Sichuan, China	this study
Bapaludina dazhouensis gen. & sp. nov. ind 8	PX111719	Tongbohe River, Tongchuan, Dazhou, Sichuan, China	this study
Dalipaludina delavayana ind 1	OQ708666	Chibihu Lake, Yunnan, China	Zhang et al. (2023)
Dalipaludina delavayana ind 2	OQ708670	Chibihu Lake, Yunnan, China	Zhang et al. (2023)
Dalipaludina occidentalis ind 1	OQ708664	Jianhu Lake, Yunnan, China	Zhang et al. (2023)
Dalipaludina occidentalis ind 2	OQ708665	Jianhu Lake, Yunnan, China	Zhang et al. (2023)
Dalipaludina oxytropoides ind 1	MZ55834	Luguhu Lake, Yunnan, China	Zhang et al. (2023)
Dalipaludina oxytropoides ind 2	MZ55835	Luguhu Lake, Yunnan, China	Zhang et al. (2023)
Anularya mansuyi	GU198773	Qiluhu Lake, Yunnan, China	Du et al. (2013)
Torotaia cf. *mainitensis*	MH319897	Lake Mainit, the Philippines	Stelbrink et al. (2019)
Sinotaia quadrata	MN998007	Luzon, the Philippines	Stelbrink et al. (2020)
Sinotaia aeruginosa	ON357987	unknown	unpublished
Sinotaia purificata	KF535371	unknown	unpublished
Sinotaia tricinctus	OQ708662	unknown	Zhang et al. (2023)
Heterogen japonica	MK308324	unknown	unpublished
Celetaia persculpta	MN997916	Sulawesi, Indonesia	Stelbrink et al. (2020)
Ussuripaludina ussuriensis	NC035754	Amur River, China	Wang et al. (2017)
Cipangopaludina chinensis chinensis	LC437761	China	Hirano et al. (2019)
Cipangopaludina longispira	GU198809	Yilonghu Lake, Yunnan, China	Du et al. (2013)
Margarya francheti	KJ636769	Jianhu Lake, Yunnan, China	Zhang et al. (2015)
Margarya melanioides	KJ636765	Jianhu Lake, Yunnan, China	Zhang et al. (2015)
Margarya dianchiensis	KJ636779	Dianchi Lake, Yunnan, China	Zhang et al. (2015)
Cipangopaludina chinensis laeta	LC028536	Japan	Hirano et al. (2019)
Anulotaia sp.	MN997905	Laos	Stelbrink et al. (2020)
Trochotaia trochoides	MN998024	Thailand	Stelbrink et al. (2020)
Bellamya crawshayi	FJ405844	Zambia	Sengupta et al. (2009)
Filopaludina sumatrensis peninsularis	KU318346	unknown	Ng et al. (2016)
Bakyietaia mutica	OQ708663	unknown	Zhang et al. (2023)
Taia sp.	MN998017	Myanmar	Stelbrink et al. (2020)
Tchangmargarya multilabiata	KJ636767	Shilin, Kunming, China	Zhang et al. (2015)
Tchangmargarya yangtsunghaiensis	KJ636772	Yiliang, Kunming, China	Zhang et al. (2015)
Viviparus contectus	FJ405835	Denmark	Sengupta et al. (2009)

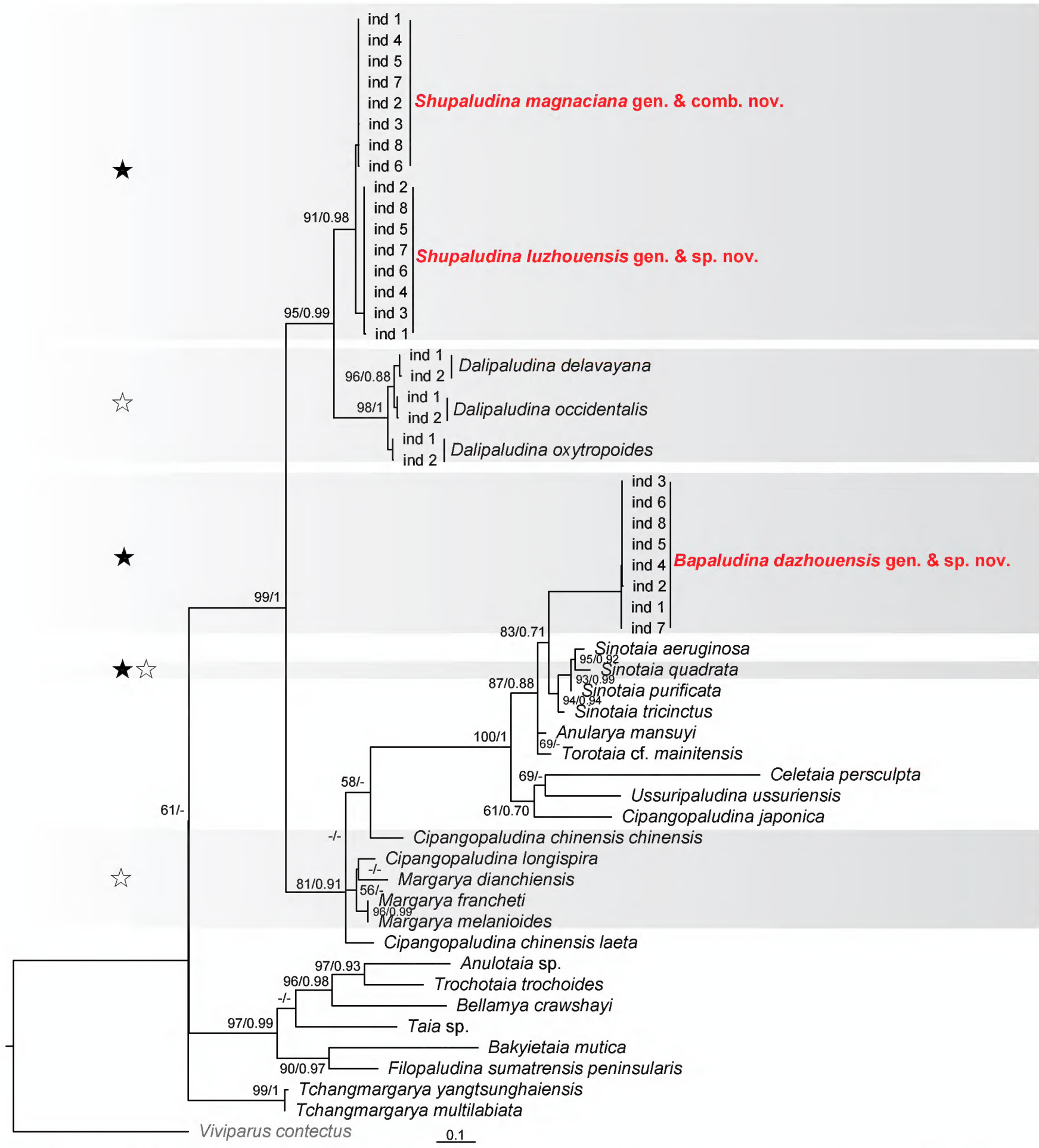

Figure 1. Maximum likelihood tree and Bayesian inference tree inferred from *COI* gene sequences. Bootstrap supports/posterior probabilities are shown on the left/right of nodes on the tree. BS below 50 and BPP below 0.70 are hidden. Shadows show the groups distributed in the upper Changjiang River; black star shows the groups' habitat in flowing water; white star shows the groups' habitat in still water.

Systematics

Family Viviparidae Gray, 1847
Subfamily Bellamyinae Rohrbach, 1937

Genus *Shupaludina* Z.-G. Chen, Y.-T. Dai, H. Chen & X.-P. Wu, gen. nov.

https://zoobank.org/5929CD54-943B-4120-9B18-F5E800CC9C2C

Figs 2, 3A, B, 4A–D, 5A, 8

Type species. *Paludina magnaciana* Heude, 1889.

Diagnosis. Shell small to medium-sized (SH 20.3–40.4 mm), relatively thick and solid; apex blunt. Whorls inflated. Suture rather deep. Teleoconch with several weak and indistinct keels. Inner lip of the aperture is folded and tightly overlapping on the columellar margin, completely covering the umbilicus and forming with growth a crescent-shaped fortification, even in juvenile specimens. Operculum rather thick, much smaller than aperture (OH/AH = 0.72–0.83), exterior surface of operculum rough, inner surface of operculum with a smooth outer ring and a rough inner ring, the nuclear region with shiny grains. Lateral and inner marginal teeth with a large, broad, and blunt central denticle and some small and sharp cusps on both sides.

Description. Shell conical, dextral, small to medium-sized (SH 20.3–40.4 mm), relatively thick, solid,

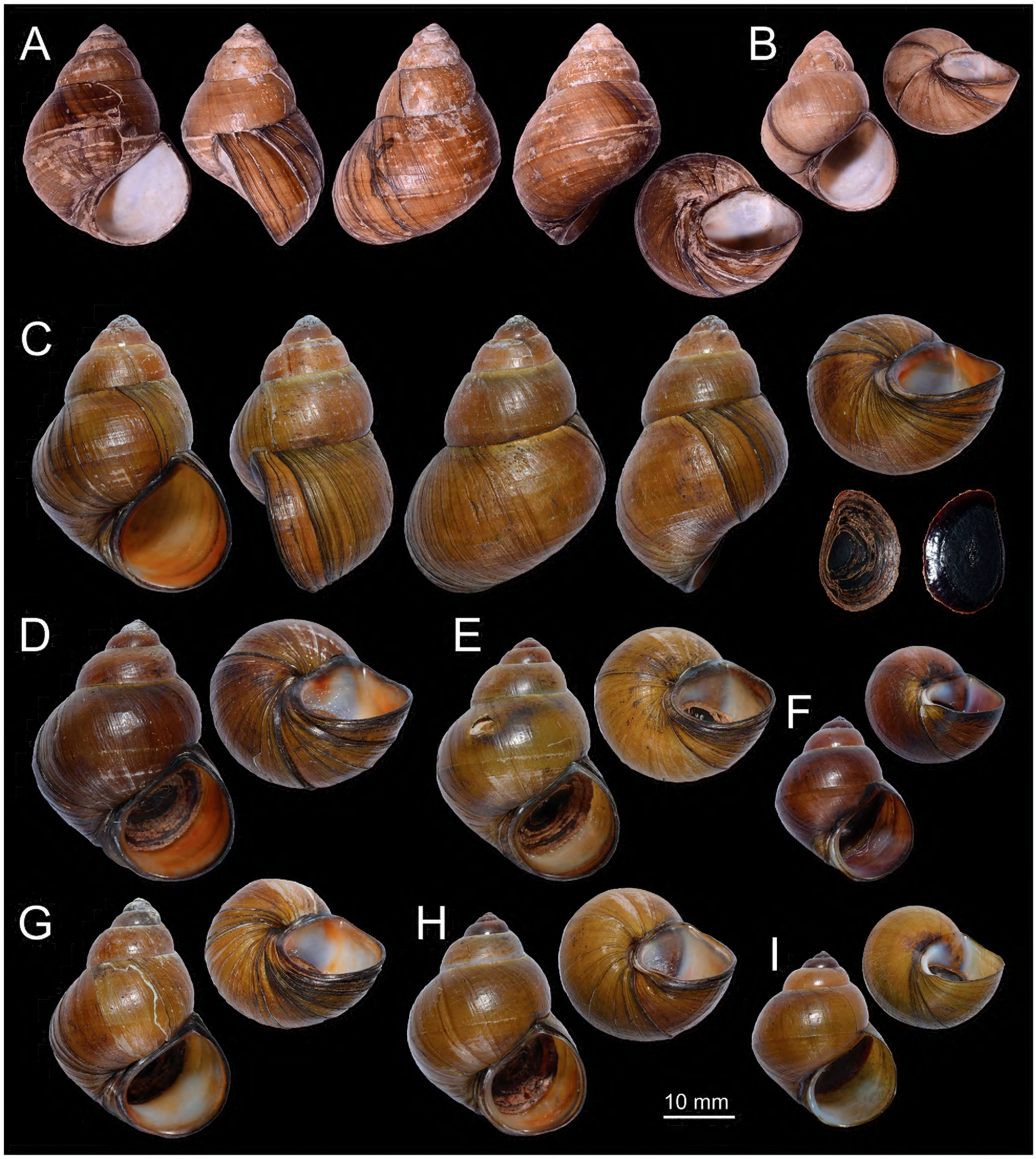

Figure 2. *Shupaludina magnaciana* gen. & comb. nov. **A, B.** Syntype, ASIZB FG492559–60; **C–I.** Partial new materials, NCUMB 19001–03, NCUMB 19061, NCUMB 19004, NCUMB 19011–12.

opaque, glossy, with 5.5–7.0 whorls in adults. Whorls inflated. Suture rather deep. Early teleoconch almost smooth or with spiral lines invisible to the naked eye, apex blunt and low. Teleoconch with several weaker and indistinct keels, without hairs, with dense growth lines. Aperture waved, ovate, oblique, more than half of shell in height. Inner shell surface orange to white. Outer lip black and thickened, inner lip of the aperture is folded and tightly overlapping on the columellar margin, completely covering the umbilicus and forming with growth a crescent-shaped fortification, even in juvenile specimens. Shell multicolored, teleoconch yellowish-green, brown, or reddish-brown, apex region darker.

Operculum much smaller than aperture (OH/AH = 0.72–0.83), corneous, ovate, rather thick, dark brown, exterior surface of operculum rough, inner surface of operculum with a smooth outer ring and a rough inner ring, the nuclear region with shiny grains.

Radular central tooth with a relatively sharp central denticle and six small and sharp cusps on both sides; lateral tooth with a large, broad, and blunt central denticle and four to five small and sharp cusps on both sides; inner

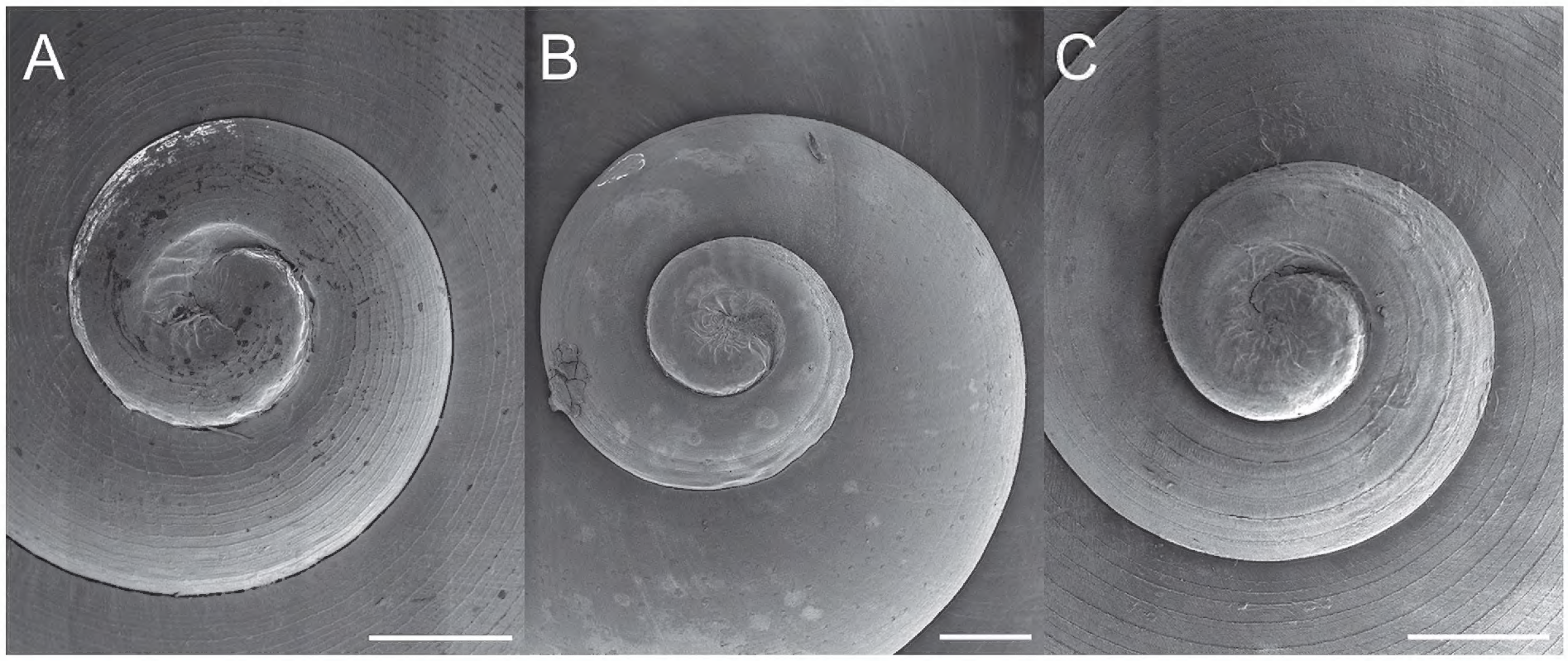

Figure 3. SEM images of the early teleoconch. **A.** *Shupaludina magnaciana* gen. & comb. nov., NCUMB 19002-1; **B**. *Shupaludina luzhouensis* gen. & sp. nov., NCUMB 25002-1; **C.** *Bapaludina dazhouensis* gen. & sp. nov., NCUMB 25018-1. Scale bar: 500 µm.

marginal tooth with a large, broad, and blunt central denticle and four to five small and sharp cusps on both sides; outer marginal tooth with 15–22 long and very sharp cusps.

Etymology. The genus name is made from the *Shu* abbreviation for Sichuan and *paludina* for river snails.

Vernacular name. 蜀田螺属 (shǔ tián luó shǔ).

Distribution and ecology. Known from the tributaries of the Minjiang River and Tuojiang River in northwestern Chengdu and the Yongninghe River in southern Luzhou (Fig. 6). Maybe distributed in the Qujiang River from eastern Sichuan to northern Chongqing. The genus may have a wider potential distribution. The first author identified similar specimens during fish surveys in the Qingyijiang River at Yaan (Fig. 6) from 2017 to 2020 but did not preserve the specimens. Living in the pebble-bottom sections of the cold and flowing tributaries with seasonal floods in sympatry with *Hua* spp., *Lithoglyphopsis* spp., and *Tricula* spp. (Fig. 6). No living animals were found in the main streams or the muddy or still-water sections of the tributaries.

Remarks. The major diagnostic characters of all six genera of Bellamyinae distributed in the upper Changjiang River Basin were shown in Fig. 5 and Table 2. In terms of morphology, *Shupaludina* gen. nov. is most similar to *Bapaludina* gen. nov. by the similar shell shape, the outward folding and tightly overlapping inner lip, and the small operculum. It can be distinguished from *Bapaludina* gen. nov. by the presence of keels on the teleoconch (vs. absence), the larger and thicker operculum (OH/AH = 0.72–0.83 vs. 0.55–0.61), the larger crescent-shaped fortification, and the larger, broader, and blunter central denticle of the lateral and inner marginal teeth. *Shupaludina* gen. nov. is somewhat similar to *Sinotaia* by the similar shell size and shape (Fig. 5), but differs by the different early teleoconch (almost smooth or with spiral lines vs. smooth but covered with hairs, although these are lost as specimens mature), the larger aperture (AH/SH > 1/2 vs. < 1/2), the outward folding and tightly overlapping inner lip (vs. thin and simple), and the operculum much smaller than aperture (vs. almost same size as aperture). In terms of molecular phylogeny, *Shupaludina* gen. nov. is the sister group of *Dalipaludina* but differs by the smaller shell, the blunt apex (vs. pointed), the larger aperture (AH/SH > 1/2 vs. < 1/2), the outward folding and tightly overlapping inner lip (vs. thin and simple), and the operculum much smaller than aperture (vs. almost same size as aperture). *Shupaludina* gen. nov. has a special overlapping inner lip and small operculum, which is similar to *Bakyietaia* Zhang, Yen & von Rintelen, 2025. The two genera can be distinguished by the different apex (blunt vs. pointed), the different early teleoconch (rounded vs. keeled), the different keels on the teleoconch (very weak vs. strong), and the larger aperture (AH/SH > 1/2 vs. < 1/2 in most species). Molecular phylogeny and isolated distributions also supported the difference between them. *Shupaludina* gen. nov. is distributed in the Changjiang River, while *Bakyietaia* is distributed in the Pearl River, the Red River, the Hainan insular rivers, and the mainland coastal rivers in southern China (Zhang et al. 2025). Yen (1938) recorded *Bakyietaia polyzonata* (Frauenfeld, 1862) in Sichuan. However, the specimens presented in the article appear to be more akin to *Sinotaia*. *Bakyietaia polyzonata* is endemic to the upper Pearl River in southwestern Guangxi and northern Vietnam (Zhang et al. 2025). *Bakyietaia wilhelmi* (Yen, 1939) recorded in Chengdu were also artificially introduced (Zhang et al. 2025).

Shupaludina magnaciana (Heude, 1889), comb. nov.

Figs 2, 3A, 4A, B, 5A

Paludina magnaciana Heude, 1889: 48 (Valle *Tchong-King*).

Paludina magnaciana - Heude, 1890: 177 (flumine *K'iu* (渠)).

Syntype. ASIZB FG492559–60, MCZ Mala 167345, Kiu-h, Se tch (= Qu County [渠县], Dazhou City [达州市], Sichuan Province [四川省]), leg. P. Magnac.

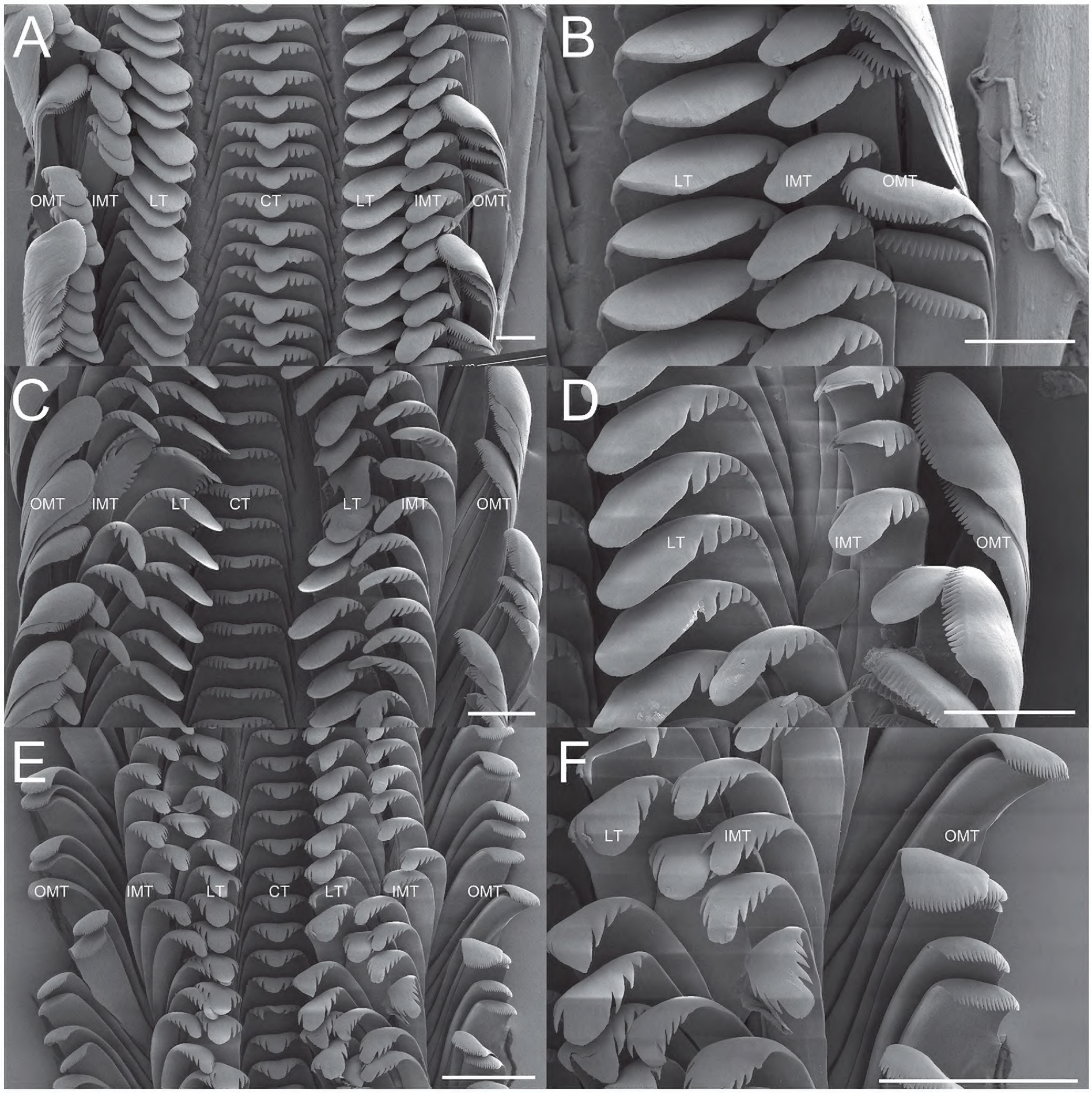

Figure 4. SEM images of the radula. **A, B.** *Shupaludina magnaciana* gen. & comb. nov., NCUMB 19002-2; **C, D**. *Shupaludina luzhouensis* gen. & sp. nov., NCUMB 25002-2; **E, F.** *Bapaludina dazhouensis* gen. & sp. nov., NCUMB 25018-2. Scale bar: 100 μm.

New materials. n = 100. NCUMB 19001–010, Baimuhe River [柏木河], Yunqiao Wetland [云桥湿地], Pidu District [郫都区], Chengdu City, Sichuan Province, China, 30.87573°N, 103.88175°E, leg. Zhong-Guang Chen, November 2019; NCUMB 19011–60, ZMNH 8009–8028, IHB 0202506001–5, SAFS 250001–5 Yangliuhe River [杨柳河], Wenjiang District [温江区], Chengdu City [成都市], Sichuan Province, China, 30.81937°N, 103.71643°E, leg. Zhong-Guang Chen, November 2019; NCUMB19061–70, Mengyanghe River [濛阳河], Mengyang Town [濛阳镇], Pengzhou City [彭州市], Chengdu City [成都市], Sichuan Province, China, 30.95389°N, 104.11625°E, leg. Zhong-Guang Chen, November 2019.

Diagnosis. Early teleoconch with dense spiral lines. Teleoconch with a weak but distinct keel at suture, above and below suture with several weak and indistinct keels. Aperture ovate. Lateral tooth with a large, broad, and blunt central denticle and four small and sharp cusps on both sides; inner marginal tooth with a large, broad, and blunt central denticle and four small and sharp cusps on both sides; outer marginal tooth with 15–16 long and very sharp cusps.

Description. Shell conical, dextral, small to medium-sized (SH 23.8–40.4 mm), relatively thick, solid, opaque, glossy, with 6.0–7.0 whorls in adults. Whorls inflated. Suture rather deep. Early teleoconch with dense spiral lines invisible to the naked eye, apex blunt and low. Teleoconch with a weak but distinct keel at suture, above and below suture with several weaker and indistinct keels, without hairs, with dense growth lines. Aperture waved, ovate, oblique, more than half of shell in height.

Table 2. Comparisons of major diagnostic characters of six genera of Bellamyinae from the upper Changjiang River.

	***Shupaludina* gen. nov.**	***Bapaludina* gen. nov.**	***Dalipaludina***	***Cipangopaludina***	***Sinotaia***	***Margarya***
Shell size	SH 20.3–40.4 mm (n = 118)	SH 22.2–32.5 mm (n = 20)	SH 40.2–65.7 mm (n = 10)	SH 55.3–70.5 mm (n = 20)	SH 22.2–37.8 mm (n = 20)	SH 65.1–87.4 mm (n = 20)
Apex	blunt	blunt	pointed	pointed	blunt	blunt
Early teleoconch	almost smooth or with spiral lines, rounded	with spiral lines, rounded	smooth, rounded	smooth but covered with hairs, although these are lost as specimens mature, weakly keeled	smooth but covered with hairs, although these are lost as specimens mature, keeled to rounded	smooth or tuberculated, rounded or keeled
Keels on the teleoconch	very weak	absent	weak to strong	weak to absent	absent to strong	weak to strong
Aperture height/shell height	> 1/2	> 1/2	< 1/2	< 1/2	< 1/2	< 1/2
Inner lip	outward folding and tightly overlapping	outward folding and tightly overlapping	thin and simple	thin and simple	thin and simple	thin and simple
Operculum	much smaller than aperture (OH/AH = 0.72–0.83)	much smaller than aperture (OH/AH = 0.55–0.61)	almost same size as aperture	almost same size as aperture	almost same size as aperture	almost same size as aperture

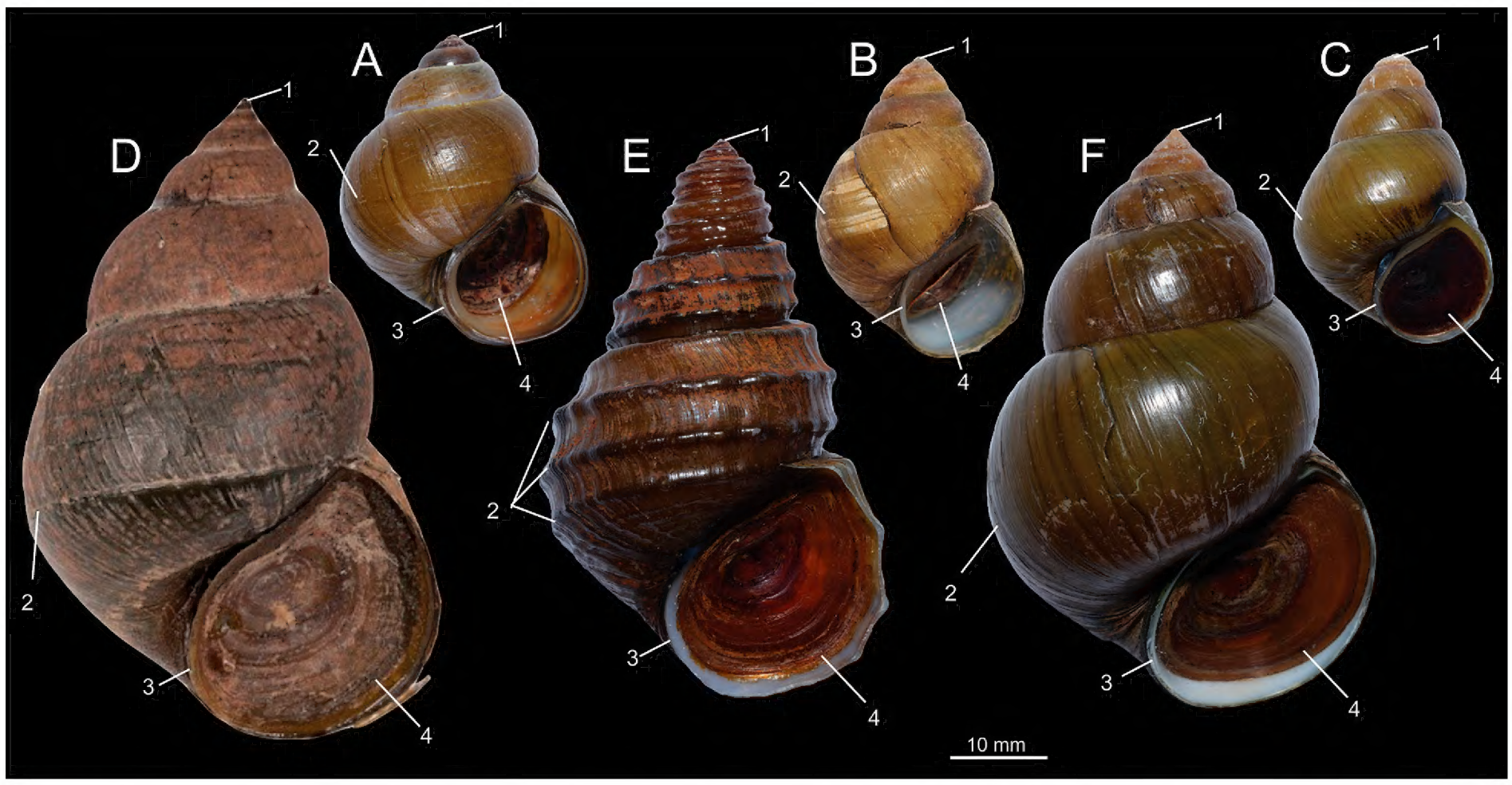

Figure 5. Comparisons of the six genera of Bellamyinae from the upper Changjiang River. **A.** *Shupaludina magnaciana* gen. & comb. nov.; **B.** *Bapaludina dazhouensis* gen. & sp. nov.; **C.** *Sinotaia quadrata*; **D.** *Dalipaludina delavayana* (Zhang et al. 2023); **E.** *Margarya monodi*; **F.** *Cipangopaludina chinensis*. 1 shows the apex; 2 shows the keels on the teleoconch; 3 shows the inner lip; 4 shows the operculum.

Inner shell surface orange to white. Outer lip black and thickened, inner lip of the aperture is folded and tightly overlapping on the columellar margin, completely covering the umbilicus and forming with growth a crescent-shaped fortification, even in juvenile specimens. Shell multicolored, teleoconch yellowish-green to reddish-brown, apex region darker.

Operculum much smaller than aperture (OH/AH = 0.72–0.83), corneous, ovate, rather thick, dark brown, exterior surface of operculum rough, inner surface of operculum with a smooth outer ring and a rough inner ring, the nuclear region with shiny grains.

Radular central tooth with a relatively sharp central denticle and six small and sharp cusps on both sides; lateral tooth with a large, broad, and blunt central denticle and four small and sharp cusps on both sides; inner marginal tooth with a large, broad, and blunt central denticle and four small and sharp cusps on both sides; outer marginal tooth with 15–16 long and very sharp cusps.

Measurements. Syntype: SH 25.1–30.9 mm, SW 18.9–23.7 mm; AH 14.0–17.8 mm, AW 10.3–12.4 mm; SW/SH = 0.75–0.77, AW/AH = 0.70–0.74, AH/SH = 0.56–0.57. New materials: SH 23.8–40.4 mm, SW 20.2–29.6 mm; AH 15.8–22.1 mm, AW 11.6–16.7 mm; OH

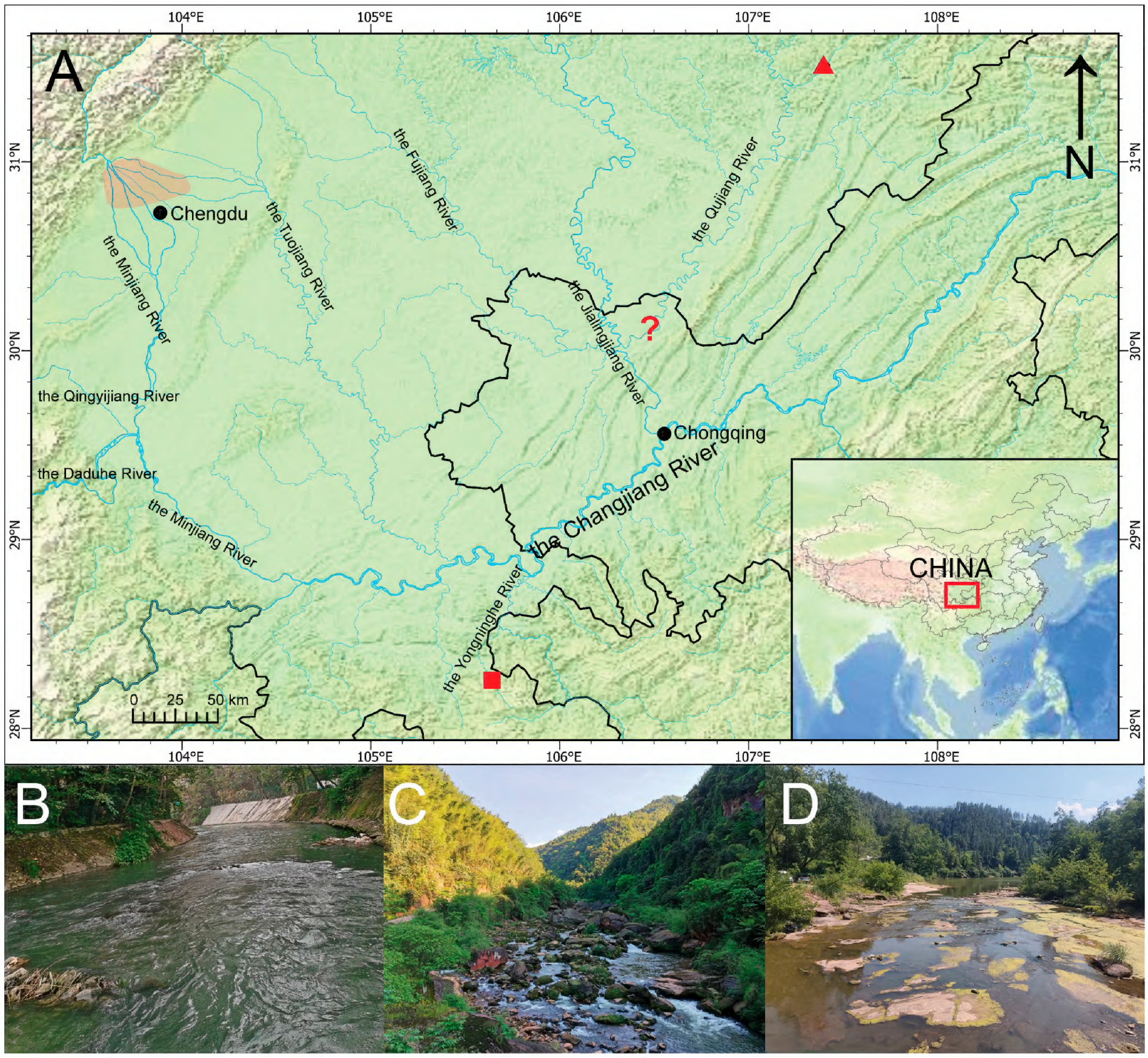

Figure 6. Distributions and habitats. **A.** Distributions: shadow shows the distribution of *Shupaludina magnaciana* gen. & comb. nov. and black triangle shows the doubtful type locality of *Shupaludina magnaciana* gen. & comb. nov., black square shows the type locality of *Shupaludina luzhouensis* gen. & sp. nov., and black triangle shows the type locality of *Bapaludina dazhouensis* gen. & sp. nov.; **B.** Habitat of *Shupaludina magnaciana* gen. & comb. nov. (taken by Xiao-Hui Mou); **C.** Habitat of *Shupaludina luzhouensis* gen. & sp. nov.; **D.** Habitat of *Bapaludina dazhouensis* gen. & sp. nov.

12.9–16.1, OW 8.3–10.8; SW/SH = 0.72–0.85, AW/AH = 0.71–0.80, AH/SH = 0.55–0.66, OH/AH = 0.72–0.83.

Vernacular name. 马氏蜀田螺 (mǎ shì shǔ tián luó).

Distribution and ecology. Currently only found in the tributaries of the Minjiang River and the Tuojiang River in northwestern Chengdu (Fig. 6). Maybe distributed in the Qujiang River Basin from eastern Sichuan to northern Chongqing. Living in the pebble-bottom sections of the cold and flowing tributaries with seasonal floods in sympatry with *Hua bailleti* (Bavay & Dautzenberg, 1910), *Lithoglyphopsis* spp., and *Tricula* spp. (Fig. 6). No living animals were found in the main streams or the muddy or still-water sections of the tributaries.

Remarks. Heude (1889) recorded the type locality of this species as "Valle *Tchong-King* (*Se-tchouan orientalis*)". Later, Heude (1890) further recorded the type locality as "in flumine *K'iu* (渠), in Yang-tze prope *Tchong-K'ing* influente". However, upon examination of the type specimen, it was found that the type locality indicated on the initial handwritten label was Kiu-h (= Kiu [渠]-hien [县], = Qu County [渠县] of Dazhou City) (Fig. 7). Qu County is located in the mountainous area of northeastern Sichuan, hundreds of kilometers away from Chongqing (*Tchong-King*), with significant environmental and aquatic animal fauna differences (Guo et al. 2021; Guo 2022). In order to find out the true type locality and distribution, we conducted a survey in Chongqing and Sichuan. Finally, we only found specimens that fit the type specimens around Chengdu (Fig. 6). We cannot determine whether the species became extinct in the Qujiang River Basin or if the type locality was incorrect.

Figure 7. Labels of the syntype of *Shupaludina magnaciana* gen. & comb. nov.

***Shupaludina luzhouensis* Z.-G. Chen & Y.-S. Guo, sp. nov.**

https://zoobank.org/72A55C58-C2BE-4891-9B29-1CFC30ED7562

Figs 3B, 4C, D, 8

Holotype. NCUMB 25001, Huagaoxi River [画稿溪], Shuiwei Town [水尾镇], Xuyong County [叙永县], Luzhou City [泸州市], Sichuan Province, China, 28.25156°N, 105.63852°E, leg. Zhong-Guang Chen, June 2025.

Paratypes. n = 15. NCUMB 25002–014, ZMNH 8029–8030, other information same as holotype.

Diagnosis. Early teleoconch almost smooth, with very weak and sparse spiral lines. Teleoconch without a weak but distinct keel at suture, but with several weak and indistinct keels. Aperture ovate, elongated. Lateral tooth with a large, broad, and blunt central denticle and five small and sharp cusps on both sides; inner marginal tooth with a large, broad, and blunt central denticle and five small and sharp cusps on both sides; outer marginal tooth with 19–22 long and very sharp cusps.

Description. Shell conical, dextral, small to medium-sized (SH 20.3–40.4 mm), relatively thick, solid, opaque, glossy, with 5.5–6.0 whorls in adults. Whorls inflated. Suture rather deep. Early teleoconch almost smooth, with very weak and sparse spiral lines, apex blunt and low. Teleoconch without a weak but distinct keel at suture, but with several weak and indistinct keels, without hairs, with dense growth lines. Aperture waved, ovate, elongated, oblique, more than half of shell in height. Inner shell surface orange to white. Outer lip brown, not thickened, inner lip of the aperture is folded and tightly overlapping on the columellar margin, completely covering the umbilicus and forming with growth a crescent-shaped fortification, even in juvenile specimens. Shell multicolored, teleoconch brown, apex region darker.

Operculum much smaller than aperture (OH/AH = 0.77–0.80), corneous, ovate, rather thick, dark brown, exterior surface of operculum rough, inner surface of operculum with a smooth outer ring and a rough inner ring, the nuclear region with shiny grains.

Radular central tooth with a relatively sharp central denticle and six small and sharp cusps on both sides; lateral tooth with a large, broad, and blunt central denticle and five small and sharp cusps on both sides; inner marginal tooth with a large, broad, and blunt central denticle and five small and sharp cusps on both sides; outer marginal tooth with 19–22 long and very sharp cusps.

Measurements. Holotype: SH 30.8 mm, SW 23.5 mm; AH 19.3 mm, AW 14.0 mm; OH 15.1, OW 10.5; SW/SH

Figure 8. *Shupaludina luzhouensis* gen. & sp. nov. **A.** Holotype, NCUMB 25001; **B–G.** Partial paratypes, NCUMB 25002–07.

= 0.76, AW/AH = 0.73, AH/SH = 0.63, OH/AH = 0.78. Paratypes: SH 20.3–32.3 mm, SW 17.6–23.6 mm; AH 14.9–20.1 mm, AW 9.6–14.2 mm; OH 11.5–15.8, OW 7.4–10.9; SW/SH = 0.73–0.87, AW/AH = 0.64–0.73, AH/SH = 0.61–0.73, OH/AH = 0.77–0.80.

Etymology. The species is named after its type locality, Luzhou.

Vernacular name. 泸州蜀田螺 (lú zhōu shǔ tián luó).

Distribution and ecology. Known from the Huagaoxi River only, a tributary of the Yongninghe River in southern Luzhou (Fig. 6). Living in the pebble-bottom sections of the cold and flowing tributaries with seasonal floods in sympatry with *Hua* sp., *Lithoglyphopsis* sp., and *Tricula* sp. (Fig. 6). No living animals were found in the main streams or the muddy or still-water sections of the tributaries.

Remarks. The new species can be easily distinguished from *Shupaludina magnaciana* comb. nov. by absence of a weak but distinct keel at suture on teleoconch (vs. presence), early teleoconch almost smooth, with very weak and sparse spiral lines (vs. with distinct and dense spiral lines), a more narrow and elongated aperture, a thinner inner lip, and more outer marginal tooth (19–22 vs. 15–16). The two species can also be distinguished by their distant and isolated distributions.

Genus *Bapaludina* Z.-G. Chen & Y.-S. Guo, gen. nov.

https://zoobank.org/F113A5D4-E017-40C4-879F-ADF8578FCE51

Figs 3C, 4E, F, 5B, 9

Type species. *Bapaludina dazhouensis* Z.-G. Chen & Y.-S. Guo, sp. nov.

Diagnosis. Shell small to medium-sized (SH 22.2–32.5 mm), relatively thick and solid; apex blunt. Whorls inflated. Suture rather deep. Teleoconch almost smooth, without keels. Inner lip of the aperture is folded and tightly overlapping on the columellar margin, completely covering the umbilicus and forming with growth a crescent-shaped fortification, even in juvenile specimens. Operculum thin, much smaller than aperture (OH/AH = 0.55–0.61), exterior surface of operculum rough, inner surface of operculum smooth. Lateral and inner marginal teeth with a small to medium, blunt central denticle and some small and sharp cusps on both sides.

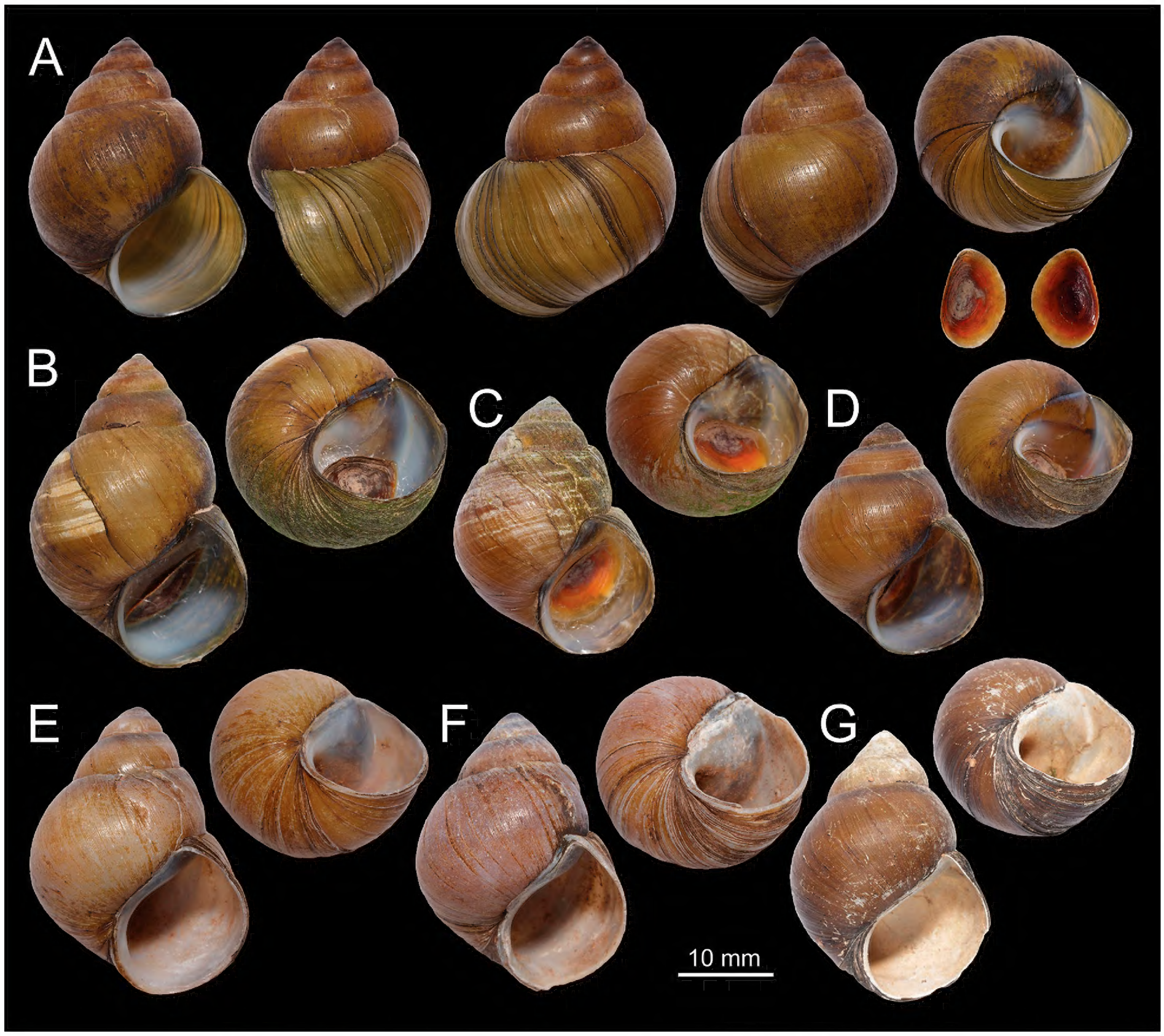

Figure 9. *Bapaludina dazhouensis* gen. & sp. nov. **A.** Holotype, NCUMB 25017; **B–G.** Partial paratypes, NCUMB 25018–20, NCUMB 25015–16, NCUMB 25021.

Description. See the species description.

Etymology. The genus name is made from "*Ba*," the abbreviation for eastern Sichuan and Chongqing, and "*paludina*" for river snails.

Vernacular name. 巴田螺属 (bā tián luó shǔ).

Distribution and ecology. Known from the tributaries of the upper Qujiang River (a tributary of Jialingjiang River) in the northern Dazhou (Fig. 6). Living in the pebble-bottom sections of the cold and flowing tributaries with seasonal floods (Fig. 6). No living animals were found in the main streams or the muddy or still-water sections of the tributaries.

Remarks. *Bapaludina* gen. nov. is the sister group of *Sinotaia* but differs by the different early teleoconch (with spiral lines vs. smooth but covered with hairs, although these are lost as specimens mature), the larger aperture (AH/SH > 1/2 vs. < 1/2), the outward folding and tightly overlapping inner lip (vs. thin and simple), and the operculum much smaller than aperture (vs. almost same size as aperture). The p-distances of *COI* sequences between *Bapaludina* gen. nov. and *Sinotaia* are 6.7%, which is larger than that between the new genus and *Torotaia* Haas, 1939 (5.0%), or *Anularya* Zhang & Chen, 2015 (5.2%).

***Bapaludina dazhouensis* Z.-G. Chen & Y.-S. Guo, sp. nov.**

https://zoobank.org/CF531ABE-02EF-4591-9F1B-C0E51FFAF46F

Figs 3C, 4E, F, 5B, 9

Holotype. NCUMB 25015, Tongbohe River [铜钵河], Qingning Town [青宁镇], Tongchuan District [通川区], Dazhou City [达州市], Sichuan Province, China, 31.50518°N, 107.40832°E, leg. Zhong-Guang Chen & Yan-Shu Guo, June 2025.

Paratypes: n = 19. NCUMB 25016–24, other information same as holotype; NCUMB 25025–34, leg. Yu-Chen Wang, June 2025, other information same.

Diagnosis. Same as the genus.

Description. Shell conical, dextral, small to medium-sized (SH 22.2–32.5 mm), relatively thick, solid, opaque, glossy, with 6.0–7.0 whorls in adults. Whorls inflated. Suture rather deep. Early teleoconch with dense spiral lines invisible to the naked eye, apex blunt and low. Teleoconch almost smooth, without keels or hairs, with dense growth lines. Aperture waved, ovate, oblique, more than half of shell in height. Inner shell surface white. Outer lip black and thickened, inner lip of the aperture is folded and tightly overlapping on the columellar margin, completely covering the umbilicus and forming with growth a crescent-shaped fortification, even in juvenile specimens. Shell multicolored, teleoconch yellowish-green to brown, apex region darker.

Operculum much smaller than aperture (OH/AH = 0.55–0.61), corneous, ovate, thin, reddish-brown, exterior surface of operculum rough, inner surface smooth.

Radular central tooth with a relatively sharp central denticle and four small and sharp cusps on both sides; lateral tooth with a medium and blunt central denticle and three small and sharp cusps on both sides; inner marginal tooth with a relatively small and blunt central denticle and four small and sharp cusps on both sides; outer marginal tooth with 18–19 long and very sharp cusps.

Measurements. Holotype: SH 29.4 mm, SW 22.8 mm; AH 18.2 mm, AW 13.3 mm; OH 10.6, OW 7.3; SW/SH = 0.78, AW/AH = 0.73, AH/SH = 0.62, OH/AH = 0.58. Paratypes: SH 22.2–32.5 mm, SW 18.5–23.7 mm; AH 15.4–19.2 mm, AW 11.1–14.2 mm; OH 8.4–11.6, OW 6.3–7.3; SW/SH = 0.75–0.83, AW/AH = 0.67–0.75, AH/SH = 0.56–0.69, OH/AH = 0.55–0.61.

Vernacular name. 达州巴田螺 (dá zhōu bā tián luó).

Distribution and ecology. Same as the genus.

Remarks. The population size of this species seems to have experienced a serious decline. Tens of thousands of empty shells were found by the river, but very few living animals were found. Living specimens are generally smaller and thinner than the empty shells (Fig. 9).

Discussion

Shupaludina gen. nov. and *Dalipaludina* have a close relationship and adjacent distributions; the former is distributed in the upper Changjiang River in Sichuan, while the latter is distributed in the same basin in Yunnan. The differentiation of them may stem from the selection of different habitats. *Shupaludina* gen. nov. is restricted to small tributaries with flowing water, whereas *Dalipaludina* is restricted to lakes with still water (Zhang et al. 2023). The abundant lakes in Yunnan have promoted the diversification of river snails that rely on still water environments, making it the region with the richest species of the family in China (Zhang 2024). In contrast, Sichuan lacks lakes, resulting in very few species of river snails having been recorded (Zhang 2024).

Although *Bapaludina* gen. nov. is a sister group with *Sinotaia*, it has evolved a similar morphology to *Shupaludina* gen. nov. The two new genera exhibit the similar overlapping inner lip, large aperture, and small operculum, which may be a convergent evolution adapted to similar rivers with seasonal floods. The overlapping inner lip can enhance the strength of the aperture, and the large aperture and small operculum can allow the soft part to retract into the depths of the shell.

The discovery of the new taxa expands our understanding of the unique river snails in the region and may suggest that the diversity of aquatic animals in Sichuan is underestimated. Taking the habitat of *Shupaludina magnaciana* gen. & comb. nov. as an example, seven new species of aquatic animals have been discovered in the same river in recent years, including five of fishes and two of mussels (Du et al. 2018; Li et al. 2020; Chen et al. 2021; Chen and Guo 2021; Wu et al. 2022, 2025; Xie et al. 2022). The small tributaries in Sichuan may contain more aquatic animal diversity and are still far from being fully explored.

As two groups highly dependent on pure flowing water, the survival of *Shupaludina* gen. nov. and *Bapaludina* gen. nov. has been severely threatened by numerous human activities. Within the Mengyanghe River, for instance, the proliferation of artificially released *Pomacea canaliculata* (Lamarck, 1822) and *Sinotaia quadrata* (Benson, 1842) has led to a significant alteration in the species composition of the habitat, with *Shupaludina magnaciana* gen. & comb. nov. becoming increasingly rare (Zhong-Guang Chen personal observation 2018–2025). Furthermore, the utilization of pesticides in the Mengyanghe River to eradicate *Tricula* sp., the intermediate host of schistosomiasis, has had a deleterious effect on the survival of the *Shupaludina magnaciana* gen. & comb. nov. (Zhong-Guang Chen personal observation 2018–2025). Following a 2022 pesticide deployment aimed at snail eradication, the first author observed a significant increase in the number of dead shells of *Shupaludina magnaciana* gen. & comb. nov. in the river. In Chengdu, a potential biodiversity hotspot, there is an urgent need to explore alternative approaches that can better balance the survival of humans and endemic species. A worse situation occurred in the Jialingjiang River Basin, the habitat of *Bapaludina* gen. nov. In the vast majority of areas here we could only find empty shells of freshwater mussels and snails. This may be due to the construction of dams causing a complete change in the environment of the entire basin. The research and protection of freshwater mussels and snails that have long been neglected in Sichuan is urgently needed.

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Supplementary material 1

The sequence alignment for the phylogenetic analyses

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Data type: fas

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Supplementary material 2

The p-distances of COI sequences between the 17 genera of Bellamyinae

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Data type: xls

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